

Scaling functional patterns of skeletal and cardiac muscles: New non-linear elasticity approach

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Abstract: Responding mechanically to environmental requests, muscles show a surprisingly large variety of functions. The studies of *in vivo* cycling muscles qualified skeletal muscles into four principal locomotor patterns: motor, brake, strut, and spring. While much effort of has been done in searching for muscle design patterns, no fundamental concepts underlying empirically established patterns were revealed. In this interdisciplinary study, continuum mechanics is applied to the problem of muscle structure in relation to function. The ability of a powering muscle, treated as a homogenous solid organ, tuned to efficient locomotion via the natural frequency is illuminated through the non-linear elastic muscle moduli controlled by contraction velocity. The exploration of the elastic force patterns known in solid state physics incorporated in activated skeletal and cardiac muscles via the mechanical similarity principle yields analytical rationalization for locomotor muscle patterns. Besides the explanation of the origin of muscle allometric exponents observed for muscles in legs of running animals and wings of flying birds, the striated muscles are patterned through primary and secondary activities expected to be useful in designing of artificial muscles and modeling living and extinct animals.

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I. INTRODUCTION

The mechanical role of muscles varies widely with their architecture and activation conditions. Striated (skeletal and cardiac) muscles are diverse in their contractive interspecific and intraspecific functional properties observed among and within animal species, nevertheless, "the smaller muscles and muscles of smaller animals are quicker". This generic feature of skeletal muscles was established by Hill [1]. More recently, the physiological adaptation of skeletal muscles resulting in beneficial changes in muscle function has been recognized by a number of investigators. It was learned that long-fibre muscles commonly contract at over larger length ranges and relatively higher velocities producing the greatest muscle forces the lowest relative energetic costs [2]. Muscles having shorter fibres expose smaller length change, but their cost of force generation is relatively less, *e.g.* [3]. Searching for determinants of evolution of shape, size, and force output of cardiac and skeletal muscle, a little is known about the regulation of directional processes of mass distribution [4,5]. Although skeletal muscles grow in length as the bones grow, most studies only involve force increasing with cross-sectional area. Following the idea that the muscle force production function is a critical evolutionary determinant [5], I develop a physical study of muscle form adaptation to a certain primary activity with growth of size preserving muscle shape.

When designing architecture of the striated muscle built from repeating units (fibres and sarcomeres) at least three distinct muscle activities should be distinguished [5]: (i) the *concentric* contraction defined as the production of active tension while the muscle is shortening and performing positive work, (ii) the *eccentric* contraction defined as the contraction during lengthening performing negative work in a controlled fashion, and (iii) the *isometric* contraction when the muscle force output is produced without changing of length and performing net work. The corresponding *mechanical work patterns* called by Russel *et al.* [5] as "concentric work" and "eccentric work" (that might be extended by "isometric work") were carefully studied via *in vivo* measurements of length-force cycling of individual skeletal muscles in active animals, such as (i) the pectoralis in flying birds, (ii) leg extensors in running cockroaches, and (iii) gastrocnemius in the level running turkey. The corresponding *muscle locomotor patterns* were called as (i) *motor*, (ii) *brake*, and (iii) *strut* functions [6].

The seminal research by Hill [1] on dynamics of electrically stimulated *isolated* muscles

was restricted to a single isotonic shortening. The studies of the corresponding motor function resulted in famous force-inverse-velocity master curve remaining the major dynamic constraint of all real (slow-fibre, fast-fibre, and superfast) muscles [7] and computationally modeled muscles, *e.g.* [8]. Besides, other two fundamental rules of muscle dynamics were noted by Hill [1]. Examining hovering humming and sparrow birds, he recognized that the "frequencies of wings are roughly in inverse proportion to the cube roots of the weights, *i.e.* to linear size". Moreover, because the linear proportionality between the stroke period and body length was found equally in electrically stimulated isolated muscles, the intrinsic *frequency-length* feature constrained by scaling rule $T_m^{-1} \propto L_m^{-1}$ beyond the nervous control is likely more universal than previously appreciated. Second *velocity-length* Hill's constraint states that "the intrinsic speed of muscle has to vary inversely to length", *i.e.* $V_m \propto L_m^{-1}$. Both Hill's scaling rules remain a challenge to viscoelastic models of transient-state mechanics and other existing theories of muscle contraction [9].

The earliest theories of muscle motor function supposed muscle to be an elastic body which, when stimulated, was converted in an active state containing elastic energy causing the muscle to shorten. Such *elastic-energy theories* failed to explain mechanisms of the force production in terms of viscoelastic characteristics. To a certain extent, poor experimental approaches providing often conflicting clues to muscle structure in relation to function may explain a little progress in understanding of contractile properties of a muscle [9,4]. Moreover, physiological muscle properties accounted for theories of muscle contractions developed at both molecular and macroscopic scales are primarily focused on the reproduction of force-velocity curve [9]. Besides, the existing phenomenological frameworks such as Hill-type muscle models only mimic the proper mechanical characteristics of muscles by means of passive viscoelastic springs attached to muscle contractive element in series [10,11,3] or in parallel [12] and recruited when muscle is activated. By ignoring the proper muscle function of force production and force transmission throughout the muscle organ, these models are able to explain no one of Hill's principal constraints in muscle dynamics. On the other hand, there exist experimental evidences of the adaptive ability of skeletal muscle to exchange *elastic* strain energy during force production [2]. In line with this concept, it has recently communicated on a possibility of the modeling of the adaptive muscle elasticity by elastic force patterns [13].

In the present paper, I develop an integrative theoretical framework to the problem of

forces, structure, and contractive non-linear dynamics in striated muscles. Instead of Hill-type modeling of *in vitro* motor function, *e.g.* [3], brake function, *e.g.* [12, 2], and strut function, *e.g.* [14], or study of muscle design by means of simulation of phenomenological force-length and/or force-velocity constraints [8], the powerful method of continuum mechanics generally providing macroscopic characterization and modeling of soft tissues, *e.g.* [15, 16], is employed. By further exploration of the elastic force patterns, I propose a self-consistent depiction of the three velocity-distinct characteristic points well distinguished in all *in vivo* force-length loops of the naturally activated muscles. Unlike the earliest elastic theories based on minimization of energy, I develop the physical concept of similarity between the force output and reaction active elastic forces that permits to avoid the details of muscle activation process. The theory is validated by a comparison to phenomenological scaling rules including both mentioned Hill's dynamic constraints and therefore may be hopefully helpful in designing artificial muscles [15] and modeling living and extinct organisms [17].

II. THEORY

A. Theoretical Background

1. McMahon's scaling models

The engineering models by McMahon [18, 19] develop previous Hill's approach to the problem of scaling of parameters of animal performance to *body weight* $W = Mg$. Using Hill's geometric similarity models [1,19] equally applied to animal body, long bone, or individual muscle, each one was approximated by a cylinder of longitudinal *length* L and *cross-sectional area* A (or diameter $D \sim \sqrt{A}$). Then, the assumption on the *weight-invariance* of for the *tissue density*, namely

$$\rho_{tiss} = \frac{M}{AL} \propto W^0, \quad (1)$$

was adopted. In mammalian long-bone allometry, this invariant was verified and observed with a high precision [20]. Mechanical models of bending bones and shortening muscles were introduced by McMahon via the weight-invariant *elastic modulus* E_{tiss} , *stress* σ_{tiss} , and *strain* ε_{tiss} , namely

$$E_{tiss} = \frac{\sigma_{tiss}}{\varepsilon_{tiss}} \propto W^0, \text{ with } \sigma_{tiss} = \frac{\Delta F}{A} \text{ and } \varepsilon_{tiss} = \frac{\Delta L}{L}. \quad (2)$$

Here $\Delta L (= L - L_0)$ is the *length change* accompanied by the *force change* $\Delta F (= F - F_0)$ counted off from the *resting length* L_0 .

While searching for functional mechanical patterns of biological systems determined by *maximal* forces using Eqs. (1) and (2), the maximal stress/strain scaling relations

$$\sigma_{geom}^{(max)} \propto W^{1/3}, \sigma_{elast}^{(max)} \propto W^{1/4}, \text{ and } \sigma_{stat}^{(max)} \propto W^{1/5}, \quad (3)$$

could be readily derived from McMahon's *geometric* (isometric), *elastic* (buckling stress) and *static* (bending elastic stress) *similarity models* distinguished through McMahon's scaling relations

$$L_{geom} \propto D, L_{elast} \propto D^{2/3}, \text{ and } L_{stat} \propto D^{1/2}. \quad (4)$$

Instead, the *maximum* stress and strain

$$\sigma_{tiss}^{(max)} \propto \varepsilon_{tiss}^{(max)} \propto W^0, \quad (5)$$

were postulated (see Table 4 in [19]) extending groundlessness his exact result for the *mean* stress $\sigma_{elast}^{(mean)} \propto W^0$, obtained within the static stress similarity model (see Fig. 1 in [19]). The improved self-consistent maximal stresses shown in Eqs. (3) follow straightforwardly from McMahon's cross-sectional areas

$$A_{geom}^{(isom)} \propto W^{2/3}, A_{elast}^{(buck)} \propto W^{3/4}, \text{ and } A_{static}^{(bend)} \propto W^{4/5} \quad (6)$$

applied to Eq. (2), along with McMahon's idea on the dominating gravitational forces in bones, muscles, and bodies, *i.e.* $\Delta F \propto gM_b \propto gM_m \propto W$. As shown in [20], the structure of long bones is driven by peak muscle forces, but not by gravity.

2. Muscle shape and structure

After Alexander [21], the *physiologic* cross-sectional area A_{0m} (PCSA) of the isolated skeletal *muscle* m of *mass* M_m composed of N bundles of masses m_i was commonly estimated, *e.g.* [22], with the help of the cylinder-geometry relation $A_i = m_i / \rho_{musc} L_i$, where L_i is directly measured muscle fibre length. The spindle-like shape of the muscle as whole organ was therefore determined by the muscle PCSA, namely

$$A_{0m} = \sum_{i=1}^N A_i = \frac{M_m}{\rho_{musc} L_{0m}}, \text{ and } \frac{1}{L_{0m}} = \frac{1}{M_m} \sum_{i=1}^N \frac{m_i}{L_i}, \text{ with } M_m = \sum_{i=1}^N m_i, \quad (7)$$

resulted in the sum of areas of muscle and the muscle length L_{0m} of the parallel-linked contractible subunits described statistically by the length-unversed sum weighed by masses. Such a coarse-grained characterization of the *muscle structure* generally ignores the arrangement of muscle fibres relative to generated force axis, distinguished by *pinnate angles*.

In scaling models, the evolution of the muscle structures across different-sized animals of *body mass* M is observed statistically via *allometric exponents* a_m , l_m , and α_m determined by common rules [21,23,25]:

$$A_{0m} \propto M_m^{a_m}, L_{0m} \propto M_m^{l_m}, \text{ and } M_m \propto M^{1+\alpha_m}, \quad (8)$$

where the *muscle mass index* α_m plays the same role as Prangel's index β in bones, as noted in [26].

When the muscle-density invariance employed implicitly in Eq. (7) and specified in Eq. (1) is applied to different skeletal muscles, the muscle shape approximated by cylinder geometry is also preserved. Consequently, the *muscle functional volume*

$$A_m L_m = A_{0m} L_{0m} = \frac{M_m}{\rho_{0m}}, \text{ with } \rho_{0m} = \rho_{musc} \propto M_m^0 \propto M^0, \quad (9)$$

holding in all muscle work loops plays the role of the mechanical muscle invariant. This condition is ensured by functional change $\Delta\rho_{musc}/\rho_{musc}$ not exceeding 5% [24]. Hence, the function-independent *muscle-shape constraint* [13]

$$a_m + l_m = 1 + \alpha_m \quad (10)$$

straightforwardly follows from Eqs. (8) and (9). Likewise the case of hindlimb mammalian bones of the mean structure $a_b^{(\text{exp})} = 2d_b^{(\text{exp})} = 0.752$, $l_b^{(\text{exp})} = 0.298$, and $\beta^{(\text{exp})} = 0.04$ [20,26], Eq. (10) is also empirically observable in muscle allometry (see analysis in Table 5 below).

B. General Muscle Characterization

1. Maximal force and stress

In *in vivo* work loops, the muscle locomotor patterns can be generally specified regardless of details of activation-deactivation conditions. In Fig. 1, the linear-slope characteristics L_{1m} can be introduced in the force-length cycling by the domains: $L_{2m} < L_{1m} < L_{3m} \approx L_{0m}$,

for the motor function, $L_{2m} > L_{1m} > L_{3m}$, for the brake function, and by $L_{2m} \gtrsim L_{1m} \gtrsim L_{3m} \approx L_{0m}$, for the strut function showing nearly isometric muscle contractions.

Place Fig. 1

Moreover, such a qualitative general characterization of the activated individual muscle m of *resting length* L_{0m} can be rationalized on the basis of common *two-point* force-length characterization, namely

$$F_{musc}^{(\text{exp})}(L_{2m}) = F_{musc}^{(\text{max})} = F_{2m} \text{ and } F_{musc}^{(\text{exp})}(L_{1m}) = F_{1m}, \quad (11)$$

introduced by the maximum force $F_{2m}^{(\text{max})}$ and the *optimum* muscle length [28, 29] L_{1m} . The *instant dynamic length* $L_m = L_{1m} \pm \Delta L_{1m}$ is counted off from the characteristic point L_{1m} via the optimum length change ΔL_{1m} (11) shown in Fig. 1 for all functions.

First, the linearization of the *in vivo* muscle force-length curve allows one to determine *trial* peak stress and corresponding strain by

$$\sigma_{musc}^{(\text{max})} = \frac{F_{musc}^{(\text{max})}}{A_{2m}} \text{ and } \varepsilon_{musc}^{(\text{max})} = \frac{\Delta L_{1m}^{(\text{max})}}{L_{2m}}, \text{ with } \Delta L_{1m}^{(\text{max})} = |L_{2m} - L_{1m}|. \quad (12)$$

The corresponding force change $\Delta F_{musc}^{(\text{max})}$ observed near the *optimum force* $F_{1m}^{(\text{max})}$ (11) provides

$$F_{musc}^{(\text{max})} = F_{musc}^{(\text{exp})}(L_{1m}) + \Delta F_{musc}^{(\text{max})} = F_{1m} + K_{musc}^{(\text{max})} \Delta L_{1m}^{(\text{max})} \quad (13)$$

that determinates *effective muscle stiffness* and *effective modulus*, respectively

$$K_{musc}^{(\text{max})} \equiv K_{2m} = \left| \frac{dF_{musc}}{dL_m} \right|_{F_{1m}^{(\text{max})}} \approx \frac{\Delta F_{musc}^{(\text{max})}}{\Delta L_{1m}^{(\text{max})}} = \frac{\Delta F_{musc}^{(\text{max})}}{F_{musc}^{(\text{max})}} E_{musc}^{(\text{max})} \frac{A_{2m}}{L_{2m}},$$

and $E_{musc}^{(\text{max})} \equiv E_{2m} = \frac{\sigma_{musc}^{(\text{max})}}{\varepsilon_{musc}^{(\text{max})}}, \quad (14)$

following from Eqs. (12) and (13).

2. Active stiffness and resonant muscle mechanics

Secondly, treating the maximum-force crossover state (11) as the generic transient-neutral state [26] the *resonant frequency* $1/T_{musc}^{(\text{max})} = T_{2m}^{-1}$ related to point 2 in Fig. 1 associated with

maximum efficiency of muscle cycling, *e.g.* [29], can also be introduced as *natural frequency* [19], namely

$$T_{2m}^{-1} \sim 2\pi \sqrt{\frac{K_{2m}}{M_m}} \sim \sqrt{\frac{E_{musc}^{(\max)}}{\rho_{0m}}} \left(\frac{\Delta F_{musc}^{(\max)}}{F_{musc}^{(\max)}} \right)^{1/2} \frac{1}{L_{2m}}, \quad (15)$$

and analyzed by Eqs. (9) and (14).

One can see that Eq. (15) yields first Hill's general constraint discussed in Introduction. However, the following three conditions are required: (i) the preservation of dynamic functional volume (9), (ii) the weight-invariance of the elastic modulus $E_{musc}^{(\max)}$ (2), and (iii) the existence of force similarity between the exerted force $F_{musc}^{(\max)}$ and its change $\Delta F_{musc}^{(\max)}$ (13). Therefore, the muscle *force-similarity principle*, namely

$$F_{musc} \cong \Delta F_{musc} \cong F_{prod} \cong F_{elast} \cong \Delta F_{elast}, \quad (16)$$

implying a coexistence of all forces in biomechanically equivalent states [26] must be adopted. Here the *active elastic force* ΔF_{elast} (shown schematically as F_{act} in Fig. 1D) is also included. The total state-transient elastic force F_{elast} is the superposition of common *passive elastic force* F_{pass} provoked by external loads and *active elastic force* ΔF_{elast} caused by the *production* force F_{prod} . The correspondence sign \cong indicates that though the involved physical characteristics belong to the same mechanical state, they may differ in both physical and numerical parameters stipulating this state.

Given that the peak *active muscle stress* σ_m always exceeds the corresponding passive stress, *e.g.* [14], in further I focus on the fully activated *transient states* described by

$$\sigma_m = \frac{\Delta F_{elast}}{A_m} = E_m \frac{\Delta L_m}{L_m}. \quad (17)$$

Unlike Eqs. (2) and (12), σ_m is the true intrinsic *elastic stress* in a certain (not specified) dynamic state. This reveals the maximum-amplitude *elastic force* of the fully activated muscle

$$\Delta F_{elast} \equiv \Delta F_m = K_m \Delta L_m = E_m A_m \frac{\Delta L_m}{L_m} \quad (18)$$

and in turn provides the corresponding *active muscle stiffness*

$$K_m = E_m \frac{A_m}{L_m}. \quad (19)$$

The underlying mechanical *sarcomere elastic stiffness* K_s is related via the muscle-volume average, namely

$$K_m = \frac{1}{A_m L_m} \int K_s(r_m) d^3 r_m, \quad (20)$$

originated from end-to-end intercellular overlapping [31, 12].

The *muscle energy change*

$$\Delta U_m \sim K_m \Delta L_m^2 \cong E_m A_m \frac{\Delta L_m^2}{L_m} \quad (21)$$

stored or released during active-period contraction provides the mechanical *cost of energy*

$$CU_m = \frac{\Delta U_m}{\Delta L_m} \cong E_m A_m \frac{\Delta L_m}{L_m}. \quad (22)$$

These relations demonstrate how the observable mechanical characteristics can be linked to the underlying muscle elastic forces using the force-similarity principle (16). In turn, the *contraction velocity*

$$V_m = \overline{V_m(t)} \equiv \frac{1}{\Delta t_m} \int_0^{\Delta t_m} \left[\frac{dL_m(t)}{dt} \right] dt \sim \left[\frac{dL_m(t)}{dt} \right]_{t=\Delta t_m} \cong \frac{L_m}{T_m} \quad (23)$$

is defined by the instant velocity $V_m(t)$ averaged over *activation time* Δt_m .

3. Fast and slow activated muscles

According to the most general classification of diverse muscles, three types are conventionally distinguished: red (slow fibre) muscles, white (fast fibre) muscles, and intermediate type, mixed fibre muscles. Although collective mechanisms of muscle contractions are poor understood, *e.g.* [32], physically, the two limiting situations of dynamic accommodation of local forces generated by cross bridge attachments can be generally rationalized. As schematically drawn in Fig. 1D, in an activated muscle, the dynamic process of equilibration between the production intrinsic forces and external loads (not shown) is followed by the spatiotemporal relaxation of elastic forces. For the simplest case of *slow muscles*, the dynamic equilibration occurs via the slow channel of relaxation, assumably common for both active, $F_{prod}^{(slow)}$, and passive elastic forces. Since passive forces in solids are short of range [33], both the forces are proportional to muscle *surface*. In contrast, it is plausible to adopt that in *fast muscles* the fast-twitch fibres transmit the locally generated forces in all directions, *i.e.* along and across fibres, resulting in the overall maximum force output $F_{prod}^{(fast)}$ to be linear with dynamic muscle *volume*. Basing on such a general physical picture, a function-independent and regime- independent characterization of the force production

function, namely

$$F_{prod}^{(fast)} \propto A_{rm} L_{rm} \text{ and } F_{prod}^{(slow)} \propto A_{rm}, \text{ with } r = 1, 2, \text{ and } 3, \quad (24)$$

is proposed via the force-size scaling rules for all three distinct states shown in Fig. 1 and hereafter distinguished by symbol r .

The widely adopted by biologists linear-displacement regime is discussed in Eq. (2) via $\Delta L \propto L$ resulted in the weight-independent strain (5). The corresponding optimum-velocity regime $r = 1$, attributed to the instant length-independent elastic strains, $\varepsilon_m^{(opt)} = |L_m - L_{3m}|/L_m \propto L_m^0$ (2) with L_m lying between L_{1m} and $L_{3m} \approx L_{0m}$, is now clarified by the scaling equations

$$E_{1m}^{(fast)} = E_{fast}^{(opt)} \propto L_m^1 \text{ and } E_{1m}^{(slow)} = E_{slow}^{(opt)} \propto L_m^0 \quad (25)$$

characteristic of fast and slow muscles. Such a muscle description follows from the similarity (16) between the active elastic force $\Delta F_{1m} = \Delta F_{elast}^{(opt)} = E_{1m} A_{1m} \varepsilon_{1m}$ (18) and corresponding production force (24). The *optimum* force-velocity muscle mechanics is rationalized below in Table 1 and then tested by empirical data.

Similarly, the bilinear-displacement regime $r = 2$ introduced by the dynamic length change $\Delta L_{2m} = |L_m - L_{1m}| \propto L_m^2$, with L_m lying between L_{2m} and L_{1m} , and the *maximum* active elastic force $\Delta F_{2m} = \Delta F_{elast}^{(max)} = E_{2m} A_{2m} \varepsilon_{2m}^{(max)}$ (18) results in the maximal elastic moduli

$$E_{fast}^{(max)} = E_{2m}^{(fast)} \propto L_m^0 \text{ and } E_{slow}^{(max)} = E_{2m}^{(slow)} \propto L_m^{-1}, \quad (26)$$

adjusted with the muscle production function (24) via the force similarity principle (16). Finally, the high-velocity trilinear regime $r = 3$ is suggested by the moderate-force and moderate-elastic muscle determined by

$$E_{fast}^{(mod)} = E_{3m}^{(fast)} \propto L_m^{-1} \text{ and } E_{slow}^{(mod)} = E_{3m}^{(slow)} \propto L_m^{-2}. \quad (27)$$

This condition specifies point 3 in Fig. 1, along with the underlying cubic-power muscle displacements $\Delta L_{3m} \propto L_m^3$ scaled by dynamic L_m lying above or below the characteristic length L_{3m} in any muscle acting as motor, brake or strut (see Fig. 1).

C. Muscle Functions

Likewise the naturally curved mammalian long bones biomechanically adapted to the maximum longitudinally bending [20, 26], the muscle *motor function* is assigned to locomotor muscles showing concentric positive work exerted by elastic bending forces. Given that the *elastic force patterns* coincide for bending and torsion [26], both kinds of unpinnate and uni-pinnate skeletal muscles, having respectively close to zero and non-zero fixed pinnate angles, may be expected to be structured by the same motor function. The specific-function mechanical characterization is described in Appendix B and results are summarized in Table 2.

III. RESULTS

A. Assumptions and predictions

The following assumptions are made regarding elastic striated muscles:

1. The muscles are considered at macroscopic scale as individual homogeneous organs. Within the continuum mechanics, the coarse-grained approach ignores the details of heterogeneous microstructure and pinnate angles.
2. When activated under different boundary loaded conditions, the muscles do not undergo changes in shape and whole volume. The emerging elastic fields follow patterns established for long solid cylinders.
3. The mechanical similarity adopted between the extrinsic forces exerted by the muscle and intrinsic elastic reaction forces, as well as the dynamic similarity adopted for contraction velocities and frequencies are observable in all biomechanically equivalent states.
4. The natural ability of the non-linear elastic tuning of fast and slow muscles to distinct locomotor states can be characterized by the elastic moduli sensitive to evolving dynamic variable associated here with the regime-characteristic muscle length.

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The function-independent mechanical characterization of muscles is provided in Table 1.

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Place Table 1.

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The specific case of muscle structure accommodation in the bilinear regime is described in Table 2.

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Place Table 2

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The rules of mass distribution across and along the muscle axis provided in Table 2 in terms of the muscle-structure scaling exponents $[a_{2m}, l_{2m}]$ are characteristic for slow, fast, and mixed muscles producing maximum force. In Table 3, these scaling rules are compared with the finding for the optimal-force state $[a_{1m}, l_{1m}]$ and moderate-force state $[a_{3m}, l_{3m}]$.

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The dynamic characteristics of distinct-velocity contractions are predicted in Table 4.

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Place Table 4

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The consequences of the theoretical scaling framework are:

1. The peak forces generated in all regimes scales as muscle volume or surface in fast or slow muscles, respectively.
2. A general, function-independent mechanical description of the striated muscle activated in the linear-displacement regime is predicted for each type of muscles (Table 1).
3. The muscle-type independent locomotor functions and related mechanical and dynamic characteristics of the striated muscle activated in the bilinear regime are predicted (Table 2).
4. The muscle-type independent varied dynamic structures are predicted for all muscle regimes and functions (Table 3).
5. The function-independent dynamic scaling characteristics are obtained in Table 4 for all type of muscles.

In what follows, all theoretical findings are tested by the available from the literature data.

IV. DISCUSSION

”What determines the shape, size, and force output of cardiac and skeletal muscle?” (Louis Sullivan quoted in [5]). The provided coarse-grained study of conservative striated muscles suggests that the size-dependent peak elastic forces determine fiber-type-independent patterns of the functionally adapted structures preserving muscle shape. The size-dependent peak force output is determined by the muscle volume and area for white and red muscles, regardless of muscle structure and function.

A. Function against structure

1. General muscle characterization

Being composed of bundles of muscle fibres including all other contractible components (neural, vascular, and collagenous reticulum), the striated muscle is thought of as a heterogeneous *continuum medium* transmitting the produced tension internally and externally, *e.g.* [34]. Primarily, I address the problem of mechanical design of striated muscle to a general, function-independent characterization of the individual muscle organ loaded by tension, reaction, and gravity through tendons, ligaments, and bones. My non-energetic approach is physically grounded by the existence of linear force-displacement regions (shown by the solid arrows in Figs. 1A, 1B, and 1C) in all *in vivo* work loops regardless of dynamic details of approaching to the maximum exerted force $F_{musc}^{(\max)}$. Hence, the mechanical characterization of the maximum-force activated muscle arises from the muscle stiffness $K_m^{(\max)}$ (14) underlaid by sarcomere stiffness $K_s^{(\max)}$ (20). Consequently, all forces involved in muscle contraction following by active and passive elastic strains allow common mechanical description (shown in Fig. 1D) not depending on their biochemical, inertial, or reaction origin.

The analytical justification of Hill’s first frequency-length constraint arises from the analysis of Eq. (15) that requires eventually the usage of the similarity between all intrinsic muscle forces, Eq. (16). The constraint $T_m^{-1} \propto L_m^{-1}$ and other mechanical characteristics for slow muscles accumulated in Table can be applied to *steady-speed* regimes of locomotion modes where all forces are generally equilibrated and controlled by slow-fibre muscles [35]. In the case of non-steady transient locomotion when fast-twitch fibres and nervous control are additionally requested [35], Hill’s first constraint transforms [by Eqs. (15) and (25)] into a new

one, $T_m^{-1} \propto L_m^{-1/2} \propto 1/V_{fast}^{(opt)}$ (Tables 1 and 4), well known for animals running with maximal *optimum* speed [36,37] $V_{run}^{(max)} \sim V_{fast}^{(opt)} \propto \sqrt{L} \propto \sqrt{L_m}$. We have therefore demonstrated how the suggested *dynamic similarity* establishes a link between the body-propulsion speed and locomotor-muscle contraction velocity, also described by Rome *et al.* [38]. Being united with the muscle-force similarity, both constraints yield *mechanical similarity*, the key principle explored in this research.

2. Maximum force output against structure and velocity

In muscle physiology, the functional effect of muscle conceptual architecture simply states that muscle force output is proportional to PCSA. The proposed study of adaptation of the muscle structure via the force production function seems to be in qualitative agreement with this statement, because in all cases exposed in Eq. (24) the muscle force output is *proportional* to A_m . Such a simplified treatment of the fast-muscle mechanics (formally substituted by that for slow muscles) arrived at the widely adopted opinion that the peak muscle stress $F_{prod}^{(slow)}/A_m$, specifying the case of slow muscles in linear dynamic regimes with $\sigma_m^{(slow)} \propto L_m^0$ (Table 1), is generic for any muscle, as already discussed in Eq. (5). Although the proposal on scaling of the maximum production force (and active stress) with muscle size (24) is a challenge for further research, the provided fairly general physical grounds are supported by empirical observations by Marden and Allen [39]. They established statistically that the maximum force output in all biological (and human-made) motors falls into two fundamental scaling laws: (i) in fast-cycling motors, presented by flying insects, bats and birds, swimming fishes, and running animals it scales as $(motor\ mass)^1$ and (ii) in slow-cycling motors, such as myosin molecules, muscle cells, and some (unspecified) "whole muscles" the force at output scales as $(motor\ mass)^{2/3}$. The "motor mass" was associated with muscle (and fuel) mass. That fact that the authors observed muscle motors from sarcomere to whole muscle organ passing through the single-fibre level of muscle organization, makes a basis for the discussed below *micro-macro scale correspondence*.

The proposed treatment of the *in vivo* force-length curves is provided for three distinct force-velocity characteristic points (shown in Fig. 1) correlated by the inequalities

$$F_{2m} > F_{1m} > F_{3m} \text{ and } V_{2m} < V_{1m} < V_{3m}. \quad (28)$$

These three generic function-independent states are associated with the linear ($r = 1$), bilinear ($r = 2$), and trilinear ($r = 3$) muscle dynamics determined via the muscle elastic moduli E_{rm} in Eqs. (25), (26), and (27), respectively. The mechanical characterization of slow and fast striated muscles is therefore provided in terms of the maximum (ΔF_{2m}), optimum (ΔF_{1m}) and moderate (ΔF_{3m}) active elastic forces developed at the measurable maximum (V_{3m}), optimum (V_{1m}), and moderate (V_{2m}) contraction velocities (Table 4). The stabilization of the dynamic regimes is expected at the natural frequencies, which also are scaled in Table 4 to the dynamic length L_{rm} .

3. Muscle functions against size and shape

Searching for answer on "what features make a muscular system well-adapted to a specific function?" [28], it has been shown preliminary [13] that such features are related to natural conditions of the stabilization or tuning to the moderate-velocity regime $r = 2$ via the mean dynamic length of the fast-twitch fibers adapted by the best way to one of the patterns of muscle locomotor functions. In this study such features specify the role of slow-twitch fibers.

The elastic-force patterns underlying concentric, eccentric, isometric, and cardiac contractions are suggested in Eqs. (35), (39), (42), and (44), respectively. The solutions to the muscle-force and muscle-shape constraints are accumulated in Table 2 as patterned functions well distinguished by the muscle *structure parameter* ($\eta_m = d \ln A_m / d \ln L_m$) established for the motor ($\eta_1 = 4$), brake ($\eta_2 = 3$), strut ($\eta_3 = \infty$) skeletal muscles, an extended by the pump ($\eta_5 = 1$) cardiac muscle and one spring ($\eta_4 = 2$) striated muscle. These structurally adapted muscles are thought of as to be suited to efficient work during powering when, respectively, shortening ($m = 1$), lengthening ($m = 2$), or remaining in the nearly isometric dynamic state ($m = 3$), high-pressure-resistant state ($m = 4$), and likely energy-saving state ($m = 5$). The found new pump function is in accord with the observation by Russel *et al.* [5] that "the heart chamber, unlike skeletal muscles, can extend in both longitudinal and transverse directions, and cardiac cells can grow in length and width", that implies $\eta_5 < \eta_1, \eta_2$, or η_3 . Given that only a few patterns exist in elastic theory of solids [26], it is not striking that the spring, brake, and motor functions resembles McMahon's "geometric", "elastic", and "static" stress similarities discussed in Eqs. (3) and (4).

In Table 3, conceivable stable dynamic structures corresponding to muscle activity in

different dynamic regimes are analyzed. As in the case of Table 2, the solutions of dynamic constraints follow from the similarity between force output (16) and elastic-force patterns. The resulting *dynamic* states are discussed in terms of the scaling exponents for the muscle *dynamic structure* $[A_{rm}, L_{rm}]$ preserving muscle shape and volume (9). Other related observable mechanical characteristics are exemplified in Tables 1 and 2. The major outcome of the analysis in Tables 2 and 3 is that both slow-twitch and fast-twitch fibres belonging to the same muscle m should manifest concerted behavior coordinated by the dynamic active elastic forces.

Another significant feature of the analysis in Table 3 is a striking prediction of the mechanical functions which are expected to be shown by a given striated muscle m of certain specialization (*primary functions* indicated by regime $r = 2$, see proof below) when its cycling dynamics is switched to regimes $r = 1$ and 3 by tuning to the corresponding natural frequencies T_{rm}^{-1} . In case of regime $r = 1$, both types of arbitrary slow muscle tuned to T_{1slow}^{-1} and fast muscle tuned to T_{1fast}^{-1} (Table 4) are expected to show maximum workloop efficiency when acting as controlled spring. In the efficient nonlinear regime $r = 3$ the slow and fast struts ($m = 3$ in Table 2) will not show another function, but any type of brakes ($m = 2$ in Table 2) will work as motors, whereas motor are expected to expose a new function, say, $m = 6$ [determined by $\eta_6 = (6/7)/(1/7) = 6$] that is closer to the brake activity ($\eta_2 = 3$) than the strut ($\eta_3 = \infty$). The cardiac muscles seem to display a crucial dynamic state, say $m = 0$ with $\eta_0 = 0$, which flattens the heart. Such predicted *secondary functions* and unusual ($m = 0$ and 6) muscles adapted to new functions is a challenge deserving further study by experimentalists.

B. Direct observation of muscle specialization

”If a muscle is specialized for a particular mechanical role how this is reflected in its architecture?” [40]. The stated problem is approached here by the comparative analysis between the muscle allometric exponents and those predicted for particular efficient activities describing the trends of biomass accommodation via PCSA and along a muscle.

1. Isolated muscles in hindlimb of mammals and birds

In Table 5, the *morphometric data* on the allometric exponents for the mean cross-sectional area $A_{0m}^{(\text{exp})}$ and length $L_{0m}^{(\text{exp})}$ of four skeletal muscles in the mammalian hindlimb for 35 quadrupedal species of body-mass domain exceeding four orders in magnitude are studied.

Place Table 5

First, let us verify the cylinder-shape similarity of skeletal muscles described by Eq. (9). The muscle mass index α_{0m} estimated in Eq. (10) via experimental data $a_{0m}^{(\text{exp})}$ and $l_{0m}^{(\text{exp})}$ is compared in Table 5 with the measured indexes $\alpha_{0m}^{(\text{exp})}$.

Place Fig. 2

In Figs. 2 and 3, the method of determination of the primary mechanical function is illustrated: the adapted muscle structure is indicated by the appropriate theoretical point located most closely to the datapoint.

Place Fig. 3

The found reliable estimates $\alpha_{0m}^{(\text{est})}$ were used then in the muscle-function analysis in Figs. 2 and 3. The established small indices α_{0m} generally validate the muscle biomechanics by proving a high-precision observation of locomotory muscle patterns via muscle morphometry and *functional physiology*. This implies that the effect of biomechanical adaptation of muscle design to active elastic forces predominates over effects of biological adaptation assigned to small $\alpha_{0m}^{(\text{exp})}$.

Secondly, the analysis in Figs. 2 and 3 indicates strong correlations between the morphometrically characterized structure of skeletal muscle and one of the primary locomotor functions described in Table 2. The primary functions indicated in Table 5 are found with a high degree of certainty. Indeed, as illustrated in Fig. 2, the deviations of distances measured along the dashed line, corresponding to a given muscle, between the datapoint

and distant challengers for the primary function, from the smallest distance indicating the primary candidate, always exceed the experimental uncertainty.

Thirdly, the found muscle mechanical specifications do not conflict with the *physiological categorization* established for joint extensors and flexors, which muscle structures are shown to be adapted to the brake and motor functions via activation of eccentric and concentric elastic forces. The found structure parameter $\eta_{plant} \approx 18$ indicates the foot support activity for plantaris as the primary function (Table 5) that is in accord with *in vivo* workloop presented in Fig. 1C. As shown in Table 3, the struts are most conservative muscles not changing their support function in non-linear regimes. In contrast, the gastrocnemius in mammals manifests their motor, strut, and brake functions in, respectively, uphill, level, and incline running of animals. Through the motor adapted structure with $\eta_{gast} \approx \eta_1 = 4$, the analysis in Fig. 3 establishes the motor activity for gastrocnemius as the primary function naturally selected for the significant mechanical task of uphill running exploring the bilinear muscle dynamics. The effective trilinear gastrocnemius-displacement dynamics is most close to the brake-like activity $\eta_6 = 6$, attributed to the secondary function of the motor experimentally observed in gastrocnemius of incline running turkey [27] and hopping tammar wallabies [24].

In Fig. 4, the overall muscle peak stress data measured in limb muscles of animals in strenuous activity, reviewed by Biewener [25], are re-examined and re-analyzed accounting for the primary functions of hindlimb muscles established in Table 5.

Place Fig. 4

The uphill-motor specialization of gastrocnemius is independently supported by the compressive-stress analysis made in Fig. 4 for fast running, jumping, and hopping mammals. The stress scaling exponents (s_m) predicted for the motor ($s_1 = 1/5$), strut ($s_3 = 0$), and control ($s_4 = 0$) functions are shown to be distinguishable in work-specific mammalian muscles described in Table 2. Hence, although the overall-function data by Biewener [25] indeed expose almost weight-independent muscle stress, earlier postulated by McMahon in Eq. (5) and only in part justified here by the slow-fibre muscles (Table 1) and strut muscles (Table 2), the analyses in Fig. 4 demonstrates how the function-specific muscle stress may serve as a new tool for the direct observation of muscle specialization ignored in all previous

overall-function analyses.

I have also investigated an interesting question: whether the primary function established for a certain leg muscle in mammals specialized to fast running coincides with that for the same muscle in birds? The pioneering data on individual leg muscles in 8 running birds, ranging in size from 0.1 *kg* quail to 40 *kg* ostrich, are analyzed in Table 6 and Fig. 5.

Place Table 6

Place Fig. 5

In running and non-running birds (Fig. 5), the *gastrocnemius* is employed as the brake and spring, in contrast to the motor function in mammals (Table 5). This is in accord with Bennett [23], who noted that "the full force-generated capacity of gastrocnemius is only used occasionally, such as during take-off, when a bird attempts to throw itself into the air". This explains our indirect observation: the primary function of the gastrocnemius in running specialists is attributed to the foot flexor in mammals and ankle extensor in birds (Table 6). In *non-running* birds, the legs are designed to control the ground locomotion (Fig. 5), whereas the wings may share motor and brake functions (Table 3), in accord with the review by Dickinson *et al.* [6].

2. Micro-macro scale correspondence

There are many striking examples when skeletal muscles expose adaptation to a specific function, *e.g.* [43, 3]. The striated muscles anatomically suited to concentric or eccentric work [2] are structurally distinct having, respectively, long thin cells or short wide cells [5]. This observation suggests the *microscopic level* of muscle-cell adaptation introduced here by

$$A_{cell}^{(conc)} > A_{cell}^{(ecent)} \text{ and } L_{cell}^{(ecent)} > L_{cell}^{(conc)} \quad (29)$$

for the *cellular* cross-sectional area A_{cell} ($\equiv A_s$) and length L_{cell} ($\equiv L_s$). Adopting these function specific trends, one may expect to observe the cell-structure parameters $\eta_s = 4$ and 3 for sarcomeres accommodated to efficient shortening or stretching of muscle as a whole.

A general question arises whether allometric coefficients of proportionality omitted above

in all structure-function power-law (scaling) relations are also attributed to active elastic strains accompanying maximum force production? Or, alternatively, other microscopically justified mechanisms, *c.f.* [44], or additional parameters (such as pinnate angle) may result in different general macroscopic consequences? Given the highly conservative nature of contractive units of *skeletal* muscles and their well pronounced organization [25], the *specific-function trends* of the muscle cross-sectional area

$$A_{strut}^{(isom)} > A_{motor}^{(conc)} > A_{brake}^{(eccen)} > A_{contr}^{(sprin)} \quad (30)$$

and muscle-fibre length

$$L_{contr}^{(sprin)} > L_{brake}^{(eccen)} > L_{motor}^{(conc)} > L_{strut}^{(isom)} \quad (31)$$

are generally expected from Table 2. The suggested trends become observable via the primary functions established in Table 5 for gastrocnemius ($m = 1$), DDF ($m = 1$), CDE ($m = 2$), and plantaris ($m = 3$), when the regression data [22] on passive-muscle structure $[A_{0m}^{(exp)}(M), L_{0m}^{(exp)}(M)]$ are taken additionally into consideration: $A_{plant}^{(exp)} > A_{gast}^{(exp)} \gtrsim A_{DDF}^{(exp)} > A_{CDE}^{(exp)}$ and $L_{CDE}^{(exp)} > L_{gast}^{(exp)} \gtrsim L_{DDF}^{(exp)} > L_{plant}^{(exp)}$, starting with $M > 1 \text{ kg}$.

Similarly, the trend for active stiffness

$$K_{strut}^{(max)} > K_{motor}^{(max)} > K_{brake}^{(max)} \text{ and, generally, } K_{fast}^{(max)} > K_{slow}^{(max)} \quad (32)$$

straightforwardly follows from Table 2. Given that the *optimum velocity* for fast fibres $V_{1m} \propto L_m^{1/2}$ (Table 1), Eq. (31) provides

$$V_{brake}^{(opt)} > V_{motor}^{(opt)} > V_{strut}^{(opt)} \quad (33)$$

Moreover, a crude estimate for the *cost energy*

$$CU_{motor}^{(max)} > CU_{strut}^{(max)} > CU_{brake}^{(max)} \quad (34)$$

follows from $CU_{fast}^{(max)} \propto M_m$ (22) and the experimental data by Pollock and Shadwick [22], $M_1^{(exp)} > M_3^{(exp)} > M_2^{(exp)}$, considered at the same body mass M . The finding (34) is in accord with the experimental observation [44]: muscles contracting nearly isometrically (strut function) generate force more economically than muscles involved in concentric work (via motor function).

3. Muscle dynamics of mammalian legs and dragonfly wings

Given that *mammalian leg extensors* are active mostly during lengthening [2], the brake primary function ($m = 2$ in Table 2) could be assigned to leg muscles specified by effective length $L_{leg} \propto M^{1/4}$ ($\alpha_{leg} = 0$ is adopted). In accord with Hill's second constraint, underlaid by the proper frequency $T_{3m}^{-1} \propto L_m^{-2}$ (Table 4), the theory predicts $V_{leg}^{(max)} \propto L_{leg}^{-1} \propto M^{-1/4}$ that results in $1/T_{leg}^{(max)} \propto L_{leg}^{-2} \propto M^{-1/16}$. Similarly, for the wing-motor muscles in *fly-ing birds* ($m = 1$ in Table 2) one should expect $V_{wing}^{(max)} \propto L_{wing}^{-1} \propto M^{-1/5}$, for contraction velocity, and $1/T_{wing}^{(max)} \propto M^{-1/25}$, for the frequency or, alternatively, $1/T_{wing}^{(opt)} \propto M^{-1/5}$, in the optimum-velocity regime (see Table 4). Hence, analytically revealed Hill's constraint becomes observable via the empirical regression data by Medler [43]: on the maximum-amplitude contraction velocities for the locomotor muscles in leg of terrestrial animals, $V_{leg}^{(exp)} \propto M^{-0.25}$, and that for wings in flying birds, bats, and insects, $V_{wing}^{(exp)} \propto M^{-0.20}$. Moreover, the experimental data by Schilder and Marden [45] of the wingbeat frequency $1/T_{wing}^{(exp)} \propto M_m^{-0.20}$ scaled by mass M_m (and length L_{0m}) of the basalar muscle in dragonflies indicate that the motor-type muscles ($L_{0m} \propto M_m^{1/5}$, see analysis in Fig. 6) were studied self-consistently in the optimum, steady-velocity motion regime.

Place Fig. 6

In the same optimum-velocity regime (Table 1), the maximum-amplitude *static force* $F_{stat}^{(exp)} \cong \Delta F_{1m}^{(slow)} \propto M_m^{2/3}$ and net *lever-system force* $F_{ind}^{(exp)} \cong \Delta F_{1m}^{(fast)} \propto M_m$ reported by Schilder and Marden [45] may be associated with the slow and fast activated fibres in the basalar muscles tuned elastically to the linear regime through the dynamic PCSA $A_{1m}^{(dyn)} \propto M_m^{2/3}$ and length $L_{1m}^{(dyn)} \propto M_m^{1/3}$. The observed dynamic force output $F_{dyn}^{(exp)} \propto M_m^{0.83}$ can be therefore suggested as the mixed-fibre force $F_{dyn}^{(pred)} \cong \Delta F_{1m}^{(mix)} \propto M_m^{5/6}$ (Table 1), *i.e.* as a compromise of the forces $F_{stat}^{(exp)}$ and $F_{ind}^{(exp)}$. These estimates challenge further analysis of the reported dynamic forces.

V. CONCLUSION

A theoretical framework for mechanical characterization of the three transient activated states of the striated muscles passing in force-length cycles through the three distinct dynamic regimes is proposed. The explicit analytical description of muscle locomotor functions and related mechanical characteristics is provided on the basis of two concepts: (i) the preservation of spindle-type shape in skeletal muscles and egg-type shape in cardiac muscles related to the preservation of dynamic muscle volume and (ii) the mechanical similarity between action and reaction forces emerging in biomechanically equivalent states. Exploring known patterns of elastic forces in continuum mechanics, the macroscopic study of the force production and its functional and structural accommodation in the loaded muscle organ as a whole provides the following major points.

1. It is demonstrated how the dynamic (frequency-velocity) constraints for muscle contractions, first observed by Hill in hovering birds and then revealed in locomotor muscles of running animals and flying birds, bats, and insects, can be derived from the generic principle of mechanical (force and velocity) similarity.

2. It is shown how relations in classical mechanics of solids can be explored in soft tissues. The study is grounded by the active-force muscle stiffness reliably derived in all muscle work loops nearby and below the maximum-amplitude exerted forces. The muscle stiffness, underlaid by sarcomere stiffness, is shown to be dependent on muscle geometry and dynamic functional variable, underlaid by elastic moduli, which encompass all contractive elements acting as an elastic continuum medium.

3. The theoretical prediction that the fast and slow muscles should generate maximum forces linear, respectively, with the muscle volume and cross-sectional area, regardless of muscle function and structure, is in part validated by the direct empirical observation of maximal forces exerted by animals and by the provided indirect observation of the adapted (primary) muscle functions in legs of mammals and birds.

4. The macroscopic structures of locomotor skeletal muscles observable directly by muscle allometry are found to be adapted to the maximum-force state, following moderate-velocity dynamic regime, instead of the expected optimum velocity regime. Such a bilinear-displacement muscle dynamics involving both fast-twitch and slow-twitch powering muscle fibres sheds light on the origin of allometric power laws and muscle specialization. The

adapted structures are examined via available empirical data: the legs are brakes in mammals and springs in non-running birds, whereas the wings are motor-brake engines in flying species. Suggested pump function for the cardiac muscles needs further experimental tests.

5. The provided study of the muscle specialization in mammalian hindlimb indicates that the properly tuned force production function is a dominated factor in the accommodation of muscle structure. This finding also indicates the predomination role of mechanical effects over biological adaptive mechanisms assigned to the relatively small muscle-mass index. As the result, a new investigation tool for indirect statistical observation of the biomechanical adaptation of individual locomotor muscles is proposed through the regression analysis of *in vivo* muscle stresses in synergists scaled across different-sized animals.

6. The assumption on that the muscle tuning muscle ability of animals can be modeled by active elastic forces via non-linear muscle elastic moduli is validated by the observation of the theoretical predictions for muscle dynamics of legs and wings in running and flying specialists. Predictions are made for the experimental modelling the primary and secondary function by tuning the cycling muscle to the corresponding natural frequency and controlling its efficiency.

7. The conservative character of architecture and related mechanical characteristics of striated muscles suggests general trends following from mechanical and shape constraints. The trends dictated by primary functions explain, in particular, why the muscles having larger fibre and sarcomere lengths and suited to efficient eccentric work, tend toward higher optimum contraction velocities, but show lower maximum stiffness and mechanical energy cost.

8. As an intriguing outcome of the analysis of maximal contraction muscle velocities and frequencies, the maximum-speed steady locomotion is revealed to be *controlled* by non-linear elasticity of slow-fibre muscles generating moderated force. This finding deserves further evaluation in finite muscle element analysis studying top speeds of living and extant animals.

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Appendix A. List of abbreviations

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PCSA - physiologic cross-sectional area

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Mathematical signs and symbols

= - common equality sign

\equiv - identity sign implying "by definition"

\approx - approximate equality sign

\sim - proportionality relation symbol omitting only numerical coefficients

\cong - here used as similarity sign supporting only physical dimension units

\propto - here used as scaling rule symbol not supporting dimension units

.

Physical and geometrical notations

α_m - muscle-mass allometric index

$\varepsilon_m^{(opt)}$ - muscle strain in the optimum dynamic regime

η_m - muscle geometry parameter

ρ_{tiss} - tissue density

$\sigma_{tiss}^{(max)}$ - peak tissue stress

ΔL - length change

ΔF - force change

Δt_m - activation timing of muscle m

A_{rm} - cross-sectional area of muscle m in passive ($r = 0$) and active ($r \neq 0$) states

a - scaling exponent for cross-sectional area

D - diameter of ideal cylinder

E_{rm} - active-muscle elastic modulus establishing the dynamic regime $r \neq 0$

e - strain scaling exponent

$\Delta F_{elast}^{(max)} = \Delta F_m^{(max)}$ - maximum active elastic force

$F_{prod}^{(fast)}$ - production force by fast muscle

$F_{motor}^{(conc)}$ - elastic force adapted to concentric work in motor muscle

$F_{musc}^{(max)}$ - maximum force exerted by muscle

K_m - active muscle stiffness

K_s - sarcomere/cellular stiffness

L - length of an ideal cylinder

L_m - variable muscle length in non-specified dynamics

L_{rm} - dynamic muscle length in the regime r

l - length exponent

m - muscle in unspecified function

M - body mass of animals

M_m - muscle mass

r - numerical parameter indicating transient dynamic states via optimum-velocity ($r = 1$), moderate-velocity ($r = 2$), and high-velocity ($r = 3$) dynamic regimes, distinct of passive muscle state ($r = 0$).

T_{rm} - period of cycling in the adapted regime r

V_{rm} - muscle contraction velocity in the dynamic regime r

W - body weight

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Appendix B. Scaling Muscle Functions

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The *motor function* is associated with the active force $F_{prod}^{(max)}$ generated during muscle shortening at moderate contraction velocity at the turning points 2 in Figs. 1A, 1B, and 1C. In *fast-fibre* muscles, the corresponding *concentric force*

$$F_{motor}^{(conc)} = F_{elast}^{(max)} = \Delta F_{2m}^{(conc)} \sim E_{2m}^{(fast)} A_{2m}^{3/2} L_{2m}^{-1} \cong F_{prod}^{(fast)} \quad (35)$$

is described by the known universal pattern of the maximal elastic forces [33] equally applied to pure bending, pure torsion, or complex bending-torsion loads subjected to long cylinder of length L_{2m} and cross-sectional area [26] A_{2m} . The exploration of Eq. (35) though Eqs. (8), (16), (24), and (26) results in the fast-muscle-force constraint $3a_m/2 - l_m = 1 + \alpha_m$. It is remarkable that the case of slow-fibre muscle, namely

$$F_{motor}^{(conc)} = F_{elast}^{(max)} = \Delta F_{2m}^{(conc)} \sim E_{2m}^{(slow)} A_{2m}^{3/2} L_{2m}^{-1} \cong F_{prod}^{(slow)} \quad (36)$$

results in the slow-muscle-force constraint $3a_m/2 - 2l_m = a_m$, which is exactly the same as fast muscle, in view of function-independent Eq. (10). Therefore, any muscle tuned to the

motor locomotor function should expose its *dynamic structure* scaled by

$$a_{motor}^{(conc)} = \frac{4}{5}(1 + \alpha_{motor}), \quad l_{motor}^{(conc)} = \frac{1}{5}(1 + \alpha_{motor}), \quad (37)$$

regardless of the fibre type content. This finding follows from both the muscle force constraints solved with the help of the function-independent muscle-shape constraint (10). Moreover, as shown in [26], the principal component of the compressive stress $\sigma_m^{(conc)}$ specifying Eq. (17) may be caused by the peak transverse-tensile *strains*

$$\varepsilon_{motor}^{(conc)} = \frac{\Delta D_m^{(max)}}{L_m} \propto M_m^{e_m}, \quad \text{with } e_m = e_{motor}^{(conc)} = \frac{a_m}{2} - l_m, \quad (38)$$

where $\Delta D_m^{(max)} \sim D_m \sim A_m^{1/2}$ is transverse muscle deformation.

Likewise, the maximum elastic *eccentric force*

$$F_{brake}^{(eccen)} = \Delta F_{2m}^{(eccen)} \sim E_{2m}^{(eccen)} A_{2m}^2 L_{2m}^{-2} \cong F_{prod}^{(fast)}, \quad (39)$$

associated with the *brake muscle function* (Fig. 1B) provides the maximum elastic stress

$$\sigma_{brake}^{(max)} = \frac{F_{brake}^{(eccen)}}{A_m} \propto M_m^{s_m}, \quad \text{with } s_m = s_{brake}^{(eccen)} = a_m - 2l_m, \quad (40)$$

following from Eqs. (17) and (39). The unique solution to both fast-muscle-force constraint, $2a_m - 2l_m = 1 + \alpha_m$, and slow-muscle-force constraint, $2a_m - 3l_m = a_m$, is

$$a_{brake}^{(eccen)} = \frac{3}{4}(1 + \alpha_{brake}), \quad l_{brake}^{(eccen)} = s_{brake}^{(eccen)} = \frac{1}{4}(1 + \alpha_{brake}). \quad (41)$$

The *strut muscle function* treated as antagonistic to both motor and brake functions drives nearly isometric contractions characteristic of small, but non-zero length change ($\Delta L_m \ll L_m$) achieved near peak forces (see Fig. 1C). This suggests the nearly *isometric force*

$$F_{strut}^{(isom)} = E_{2m}^{(isom)} \varepsilon_{2m}^{(isom)} A_{2m} \cong F_{prod}^{(fast)}, \quad \text{with } \varepsilon_{2m}^{(isom)} = \Delta L_{2m}^{(isom)} / L_{2m}, \quad (42)$$

in fast muscles. Again, one solves the *muscle strut* constraints $2a_m + l_m = 1 + \alpha_m$ and $2a_m + 2l_m = a_m$ resulting in

$$a_{strut}^{(isom)} = 1 + \alpha_{strut} \quad \text{and} \quad l_{strut}^{(isom)} = s_{strut}^{(isom)} = 0, \quad \text{with } \Delta L_{2m}^{(isom)} \propto L_{2m}^2, \quad (43)$$

for any type of muscles.

A new antagonist (to strut muscle) tuned to the *cardiac* type contractions via active elastic force

$$F_{pump}^{(card)} = \Delta F_{2m}^{(card)} \sim E_{2m}^{(card)} L_{2m}^2 \cong F_{prod}^{(fast)} \quad (44)$$

is associated with, say, *pump function* providing the fast-muscle-force constraint $2l_m = 1 + \alpha_m$. This yields

$$a_{pump}^{(card)} = l_{pump}^{(card)} = s_{pump}^{(card)} = e_{pump}^{(card)} = \frac{1}{2}(1 + \alpha_{pump}), \quad (45)$$

equally applied to slow-fibre muscles resulting in the slow-force constraint $l_m = a_m$.

To complete the intrinsic-force description, the spring-type *control function* associated with the optimum-regime elastic force

$$F_{contr}^{(sprin)} = F_{elast}^{(opt)} \propto E_{1m}^{(slow)} M_m^{2/3} \propto E_{1m}^{(slow)} A_m^{2/3} L_m^{2/3} \cong F_{prod}^{(slow)} \quad (46)$$

in slow-fiber muscles results in

$$a_{cont}^{(sprin)} = \frac{2}{3}(1 + \alpha_{cont}), \quad l_{cont}^{(sprin)} = \frac{1}{3}(1 + \alpha_{cont}), \quad \text{with } s_{cont}^{(sprin)} = e_{cont}^{(sprin)} = 0, \quad (47)$$

that follows from the slow-force and fast-force constraints $2(a_m + l_m)/3 = a_m$ and $(2a_m + 5l_m)/3 = 1 + \alpha_m$ and therefore is valid for any type of muscle tuned to velocity-optimum regime. All obtained specific-function mechanical characteristics are summarized in Table 2.

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Figure Captions

Fig. 1. The qualitative analysis of the *in vivo* muscle force-length data. The muscle *motor function* is presented by gastrocnemius powering during shortening in uphill running turkey (*inset A*, adapted from [27]). The lateral gastrocnemius and plantaris act as brake (*inset B*) and strut (*inset C*) in hopping tammar wallabies [24]. The solid (and dashed) *arrows* indicate raising (and decreasing) of the exerted force near its maximum magnitude F_{\max} . The regions of the linear force-length domain are displayed by the force change ΔF_{1m} and length change ΔL_{1m} , both estimated from L_{1m} , and the starting datapoint F_{1m} of the force enhancement achieved at the optimum contraction velocity V_{opt} . Similar to physical pendulum, the resting length L_{0m} is expected to be passed at near maximum velocities V_{\max} and lower forces F_{3m} . The origin of intrinsic muscle forces (*inset D*): in both cases of the powering shortening (*motor*) and lengthening (*brake*) muscles the resulted force F_{\max} is a superposition of the production force output F_{prod} and reaction passive F_{pass} and active F_{act} *elastic* forces [see also text below Eq. (16)].

Fig. 2. The indirect observation of the primary activity of mammalian plantaris. The *solid symbol* is the datapoint [22] presented in Table 5 and the bars indicate experimental error. The *open symbols* are theoretical estimates for stable dynamic structures established for the motor, brake, strut, or control functions described in Table 2, with $\alpha_m = \alpha_{0m}^{(est)}$ taken from Table 5.

Fig. 3. The observation of the primary mechanical function in some isolated individual muscles in mammals. The analysis and notations correspond to those in Fig. 2. The experimental (and theoretical) data for gastrocnemius, DDF (deep digital flexor), and CDE (common digital extensor) are shown, respectively, by the closed (and open) inverted triangles, regular triangles, and circles. All the data are taken from Table 5.

Fig. 4. The qualitative study of the *in vivo* data on the peak stress in individual leg muscles of animals in strenuous activity. The symbols employed above in Figs. 2 and 3 are extended by the *open circles* (triceps) for the data on peak muscle stress taken from Table 1 in [25], with the exclusion of the slow-mode data on cantering goat and trotting cat.

The data [41] on the activated isometric stress in isolated white rabbit tibialis are added. The *dashed line* shows the brake-functional stress indicated by the stress scaling exponent $s = 1/4$. The *solid lines* are drawn by $115 \cdot M^{1/5}$, for the motor function, and by 215 kPa , for the strut and spring functions. All coefficients are adjusted by eye.

Fig. 5. The analysis of the primary mechanical functions for leg muscles in running and non-running birds. The measured (and estimated) data taken from Table 6 (and Table 2) for gastrocnemius, femorotibialis, and digital flexors are shown by the closed (and open) inverted triangles, circles, and regular triangles, respectively. The semi-open triangles are the data by Bennett [23] for non-running birds.

Fig. 6. The qualitative scaling of the basalar structure to muscle mass in male dragonflies (Odonata and Anisoptera, listed in Fig. 5 in [45]). The datapoints for muscle length $L_{0m}^{(\text{exp})}$ is a courtesy by the authors. The estimated muscle cross-sectional area $A_{0m}^{(\text{est})}$ is obtained on the basis of Eq. (1) taken with $\rho_{\text{muscle}}^{(\text{exp})} = 1060 \text{ kg/m}^3$ [46]. The *solid lines* are $L_{\text{motor}} = 0.052 \cdot M_m^{1/5}$ and $A_{\text{motor}} = 0.018 \cdot M_m^{4/5}$. The *dashed lines* indicated by the scaling exponents are drawn according to muscle specialization shown in Table 2. All pre-exponential coefficients are adjusted by eye.

Tables

Optimum muscle characteristics, (equations)	Fast fibres	Slow fibres	Mixed fibres
Optimum length change, ΔL_{1m} , (25)	L_m	L_m	L_m
Production/active-elastic force, ΔF_{1m} , (16), (18), (25)	$A_m L_m$	A_m	$A_m L_m^{1/2}$
Optimum stiffness, $K_{1m} = E_{1m} A_{1m} / L_{1m}$, (19)	A_m	$A_m L_m^{-1}$	$A_m L_m^{-1/2}$
Optimum elastic stress, $\sigma_{1m} = \Delta F_{1m} / A_{1m}$, (17)	L_m	L_m^0	$L_m^{1/2}$
Contraction frequency, $T_{1m}^{-1} \sim \sqrt{E_{1m} / \rho_{0m}} / L_{1m}$, (15)	$L_m^{-1/2}$	L_m^{-1}	$L_m^{-3/4}$
Optimum velocity, $V_{1m} = V_{musc}^{(opt)}$, (23)	$L_m^{1/2}$	L_m^0	$L_m^{1/4}$
Optimum power, $P_{1m} = F_{1m} V_{1m}$	$A_m L_m^{3/2}$	A_m	$A_m L_m^{3/4}$

Table 1. General mechanical characteristics of the striated muscles tuned to linear-displacement dynamic regime scaled to dynamic fiber length $L_m = L_{1m}$. The *mixed-fibre* scaling dynamic exponents (shown in the last column) are modeled by the common means for the fast-muscle and slow-muscle exponents (established in the second and third columns), *i.e.* $F_{mix} \sim \sqrt{F_{fast} F_{slow}}$; A_m and L_m are attributed to the stabilized *dynamic* muscle geometry constrained by muscle volume (9).

Locomotor pattern, regime (equation)	Motor, r=2 (37)	Brake, r=2 (41)	Strut, r=2 (43)	Control, r=1 (47)	Pump, r=2 (45)
Force pattern, muscle (equation)	$F_{motor}^{(conc)}$, m=1 (35)	$F_{brake}^{(eccen)}$, m=2 (39)	$F_{strut}^{(isom)}$, m=3 (42)	$F_{contr}^{(sprin)}$, m=4 (46)	$F_{pump}^{(card)}$, m=5 (44)
Maximum force output, (24)	$1 + \alpha_1$	$1 + \alpha_2$	$1 + \alpha_3$	$\frac{2}{3}(1 + \alpha_4)$	$1 + \alpha_5$
Muscle fibre length, (8)	$\frac{1}{5}(1 + \alpha_1)$	$\frac{1}{4}(1 + \alpha_2)$	0	$\frac{1}{3}(1 + \alpha_4)$	$\frac{1}{2}(1 + \alpha_5)$
Cross-sectional area, (8)	$\frac{4}{5}(1 + \alpha_1)$	$\frac{3}{4}(1 + \alpha_2)$	$1 + \alpha_3$	$\frac{2}{3}(1 + \alpha_4)$	$\frac{1}{2}(1 + \alpha_5)$
Structure parameter, $\eta_m = a_m l_m^{-1}$	4	3	∞	2	1
Length change*, (13)	$\frac{2}{5}(1 + \alpha_1)$	$\frac{1}{2}(1 + \alpha_2)$	0	$\frac{1}{3}(1 + \alpha_4)$	$1 + \alpha_5$
Maximum stress/strain*, (12)	$\frac{1}{5}(1 + \alpha_1)$	$\frac{1}{4}(1 + \alpha_2)$	0	0	$\frac{1}{2}(1 + \alpha_5)$
Maximum stiffness*, (19)	$\frac{3}{5}(1 + \alpha_1)$	$\frac{1}{2}(1 + \alpha_2)$	$1 + \alpha_3$	$\frac{1}{3}(1 + \alpha_4)$	0
Natural frequency*, (15)	$-\frac{1}{5}(1 + \alpha_1)$	$-\frac{1}{4}(1 + \alpha_2)$	0	$-\frac{1}{3}(1 + \alpha_4)$	$-\frac{1}{2}(1 + \alpha_5)$
Energy change*, (21)	$\frac{7}{5}(1 + \alpha_1)$	$\frac{3}{2}(1 + \alpha_2)$	$1 + \alpha_3$	$1 + \alpha_4$	$2(1 + \alpha_5)$
Moderate velocity* (23)	0	0	0	0	0

Table 2. The locomotor functions and their mechanical characteristics scaled to dynamic structures. The all-type powering individual muscles $m = 1, 2, 3$, and 5 are tuned to the maximum-force bilinear dynamic regime $r = 2$ [described in Eq. (26)] and muscles $m = 4$ act in the linear regime $r = 1$ [Eq. (25)]. *The data shown for fast muscles. The allometric exponents are related to animal’s body mass via Eq. (8).

Dyn. regimes	Force	Func.	Structure	Func.	Structure	Func.	Structure	Func.	Structure
$r = 1, 2, 3$	$F_{prod}^{max} \propto$	$F_{motor}^{conc} \propto$	$a_m \quad l_m$	$F_{brake}^{eccen} \propto$	$a_m \quad l_m$	$F_{strut}^{isom} \propto$	$a_m \quad l_m$	$F_{plun}^{card} \propto$	$a_m \quad l_m$
$E_{1m}^{(slow)} \propto L_m^0$	A_m	$A_m^{\frac{3}{2}} L_m^{-1}$	$\frac{2}{3} \quad \frac{1}{3}$	$A_m^2 L_m^{-2}$	$\frac{2}{3} \quad \frac{1}{3}$	A_m	$nc \quad nc$	L_m^2	$\frac{2}{3} \quad \frac{1}{3}$
$E_{1m}^{(fast)} \propto L_m$	$A_m L_m$	$A_m^{\frac{3}{2}}$	$\frac{2}{3} \quad \frac{1}{3}$	$A_m^2 L_m^{-1}$	$\frac{2}{3} \quad \frac{1}{3}$	$A_m L_m$	$nc \quad nc$	L_m^3	$\frac{2}{3} \quad \frac{1}{3}$
$E_{2m}^{(slow)} \propto L_m^{-1}$	A_m	$A_m^{\frac{3}{2}} L_m^{-2}$	$\frac{4}{5} \quad \frac{1}{5}$	$A_m^2 L_m^{-3}$	$\frac{3}{4} \quad \frac{1}{4}$	$L_m^{-1} A_m$	1 0	L_m^1	$\frac{1}{2} \quad \frac{1}{2}$
$E_{2m}^{(fast)} \propto L_m^0$	$A_m L_m$	$A_m^{\frac{3}{2}} L_m^{-1}$	$\frac{4}{5} \quad \frac{1}{5}$	$A_m^2 L_m^{-2}$	$\frac{3}{4} \quad \frac{1}{4}$	A_m	1 0	L_m^2	$\frac{1}{2} \quad \frac{1}{2}$
$E_{3m}^{(slow)} \propto L_m^{-2}$	A_m	$A_m^{\frac{3}{2}} L_m^{-3}$	$\frac{6}{7} \quad \frac{1}{7}$	$A_m^2 L_m^{-4}$	$\frac{4}{5} \quad \frac{1}{5}$	$L_m^{-2} A_m$	1 0	L_m^0	0 1
$E_{3m}^{(fast)} \propto L_m^{-1}$	$A_m L_m$	$A_m^{\frac{3}{2}} L_m^{-2}$	$\frac{6}{7} \quad \frac{1}{7}$	$A_m^2 L_m^{-3}$	$\frac{4}{5} \quad \frac{1}{5}$	$A_m L_m^{-1}$	1 0	L_m^1	0 1

Table 3. Locomotor functions predicted by dynamic structured for slow and fast striated muscles tuned to distinct dynamic regimes. The primary functions ($r = 2$) are shown by bold type. The analysis of functional muscle structures made in terms of elastic-force patterns:

the active-muscle optimum-velocity ($r = 1$), moderate-velocity ($r = 2$), and high-velocity ($r = 3$) dynamic regimes are described in the first column via the muscle elastic moduli E_{rm} [Eqs. (25), (26), and (27)] and specified by slow and fast force output [Eq. (24)], shown in the second column. The third and next odd columns show the elastic force functional scaling in concentric, eccentric, isometric, and pump contractions. The corresponding solutions to scaling equations underlaid by the force similarity principle (16) are shown for simplicity with $\alpha_{rm} = 0$, in the forth and next even columns. *Notation:* *nc* indicates non-conclusive solution.

Dynamic regimes	Optimum, $r = 1$		Moderate, $r = 2$		Maximum, $r = 3$	
Muscle type	slow	fast	slow	fast	slow	fast
Natural frequency, Eq. (15)	L_m^{-1}	$L_m^{-1/2}$	$L_m^{-3/2}$	L_m^{-1}	L_m^{-2}	$L_m^{-3/2}$
Contraction velocity, Eq. (23)	L_m^0	$L_m^{1/2}$	$L_m^{-1/2}$	L_m^0	L_m^{-1}	$L_m^{-1/2}$

Table 4. Dynamic characterization of the red (slow) and white (fast) striated muscles in the optimum-, moderate-, and maximum-velocity dynamic regimes $r = 1, 2$, and 3 described in Table 3.

Individual mammalian muscles	$a_{0m}^{(\text{exp})}$	$l_{0m}^{(\text{exp})}$	$\alpha_{0m}^{(\text{exp})}$	η_{0m}	$\alpha_{0m}^{(\text{est})}$	a_m	l_m	Prim. functions
Gastrocnemius (and soleus)	$0.77 \pm .02$	$0.21 \pm .02$	-0.03	3.7	-0.02	0.78	0.20	motor, $m = 1$
Deep digital flexor (DDF) ^{*)}	$0.85 \pm .03$	$0.18 \pm .02$	0.03	4.7	0.03	0.82	0.21	motor, $m = 1$
Comm. digit. extensor (CDE)	$0.69 \pm .04$	$0.24 \pm .02$	-0.07	2.9	-0.07	0.70	0.23	brake, $m = 2$
Plantaris (SDF)	$0.91 \pm .04$	$0.05 \pm .04$	-0.03	18	-0.04	0.96	0.00	strut, $m = 3$
Ankle-joint muscle group	$0.81 \pm .03$	$0.17 \pm .03$	-0.03	4.8	-0.03	0.78	0.19	motor, $g = 1$

Table 5. The analysis of the allometric data by Pollock and Shadwick [22] provided on the basis of Eq. (10) and Table 2. The shown statistical error is approximated by the symmetrized 95% confidence interval. The methodology of the analysis is illustrated in Fig. 2. The primary functions found in Figs. 2 and 3 are described following Table 2, with $\alpha_m = \alpha_{0m}^{(\text{est})}$. The overall muscle group ($g = 1$) is determined as the standard mean over all muscles. ^{*)}DDF includes individual flexor hallucis and flexor digitorum longus; SDF means superficial digital flexor.

Running birds	$a_{0m}^{(\text{exp})}$	$\alpha_{0m}^{(\text{exp})}$	$l_{0m}^{(\text{est})}$	$a_{0m}^{(\text{exp})}/l_{0m}^{(\text{est})}$	a_{2m}	l_{2m}	Primary function/force
Gastrocnemius	0.81 ± 0.14	0.14	0.33	2.5	0.85	0.29	brake/eccentric
Digital flexors (DF)	0.76 ± 0.22	-0.03	0.21	3.6	0.78	0.19	motor/concentric
Femorotibialis	0.80 ± 0.12	-0.02	0.18	4.4	0.78	0.20	motor/concentric
Overall group	0.79 ± 0.16	0.03	0.24	3.3	0.77	0.26	brake/eccentric

Table 6. The analysis of the allometric data by Maloiy *et al.* [42]. The shown large error is due to relatively wide confidence limits. The mean exponents $l_{0m}^{(\text{est})}$ are estimated via Eq. (10). The overall muscle group is determined as the standard mean over all muscles. The indicated primary functions and active elastic forces are described by the evaluated dynamic-structure exponents a_{2m} and l_{2m} found as most close to the experimental resting-volume data on $a_{0m}^{(\text{exp})}$ and $l_{0m}^{(\text{exp})}$ and therefore assigned to regime $r = 2$ (Table 2).

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